Neuroptera (Insecta) in amber from the Lower Cretaceous of Lebanon

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Synopsis

Glaesoconis fadiacra sp. nov. (Coniopterygidae), *Banoberotha enigmatica* gen. et sp. nov. (Berothidae) and *Paraberotha acra* gen. et sp. nov. (Berothidae) are described from Lebanese amber.

Material and techniques

In recent years the Lebanese amber has aroused considerable interest (Schlee & Dietrich 1970, Schlüter 1976) as the oldest known amber with insect inclusions. Recently the British Museum (Natural History) received some Lebanese amber from Professor Aftim Acra of Beirut, who has been processing and studying the amber for some years.

The material has been variously dated as Aptian or Neocomian, with ages ranging from 100 to 130 m.y. (Acra *et al.* 1972, Schlüter 1976).

A preliminary examination of the insect inclusions has been made, but the plant fragments and other inclusions have not been studied. Schlee (1970) points out that the amber is difficult to handle; it is very fragile and often fragmented with many cracks developed inside the pieces. These cracks affect the clarity of the amber and its strength, and various clearing and polishing techniques have been developed to make the inclusions clearer.

The amber varies in colour from pale yellow to dark red, and in a number of examples there is evidence of some flow of the amber after the insects were trapped. In these cases parts of single insects may be separated by several millimetres or more. It is not possible to determine whether the flowing of the amber took place as the insects were trapped, resulting in the head, thorax and abdomen being separated in the same lump of amber, or whether the amber melted and flowed long after the insects were trapped. The flow within one piece of amber does not always occur in the same plane and the pieces of a single insect may be separated in three dimensions.

The amber can be examined dry or by immersion in liquids. Some organic solvents (e.g. toluene, xylene) rapidly attack the amber and usually 70% alcohol or glycerin was used. Alcohol spreads through the cracks, giving better visibility, but can lead to further fractures; it will also slightly attack the amber. Polishing the surface was done with a jewellery burnishing paste which gave satisfactory results. For greater resolution some of the more fragile pieces were embedded in plastic and then mechanically polished. In some cases minute contraction of the embedding plastic can occur as it hardens. Even slight pressure resulted in the collapse of some of the amber along the fault-cracks, distorting the block.

Other examination methods included the standard microscopical preparation techniques. The amber, after briefly soaking in xylene, was embedded in Canada balsam. This produced mixed results, generally proving satisfactory but occasionally the balsam was found partially to dissolve the amber, causing slight fragmentation of the insect specimen. A similar result was obtained by embedding in Euparal, but here the Euparal tended to clear the amber considerably, improving visibility of the specimen. The fragmentation does not destroy the fossil but results in the chitin being apparently stretched slightly in all directions by the solution effect of the mountant. This breaks the insect up into a series of small blocks which together retain the original shape of the fossil. The result is similar to a newspaper picture; at low magnification the picture is clear but at high magnification the individual particles can be seen. Some details become clearer in this manner but the specimens should always be studied fully before embedding. In this way any minor loss of detail may be more than compensated for by the improved definition of other parts.

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Specimens did not always fragment when embedded in Euparal and embedding can result in dramatically improved visibility of the specimen.

Small pieces embedded in 'Trylon' resin have been cut into serial sections on a Lastac wire saw using a 0·008-inch (0·2 mm) diamond-impregnated wire. The results have been promising but care is needed in handling the sections owing to the fragility of the amber.

Preliminary infra-red spectroscopic examination has shown a spectrum clearly distinct from that of Baltic amber and copals.

Systematics

From the amber collected by Professor Acra and at present being studied at the British Museum (Natural History), twelve orders of insects and three of Arachnida (Pseudoscorpions, Mites, Spiders) have been recognized. By far the most abundant insects in the amber are the Nematoceran Diptera, with the Hemiptera–Homoptera next, a high proportion of which are Aleyrodidae. Specimens of the following Orders have been found in the sample from Professor Acra: Thysanura, Collembola, Orthoptera, Dictyoptera, Psocoptera, Hemiptera, Thysanoptera, Neuroptera, Lepidoptera, Hymenoptera, Coleoptera and Diptera.

An account of the Lepidoptera in Lebanese amber has been published (Whalley 1977, 1978); in the present paper the Neuroptera are described.

Six specimens of neuropterous insects have been identified in the sample of Lebanese amber. These are two Coniopterygidae, three Berothidae and one fragment, probably referable to the Myrmeleonidae. No Neuroptera were recorded from Lebanese amber by Schlüter (1976), but he found specimens in resins of Cretaceous age from France (Schlüter 1975).

Family **MYRMELEONIDAE** ?

One of the specimens is only fragments of a wing (Figs 1–2), possibly a Myrmeleonid, but there is insufficient evidence to be certain of this determination. The group is known from the Triassic onwards (Crowson *et al.* 1967).

Family **CONIOPTERYGIDAE**

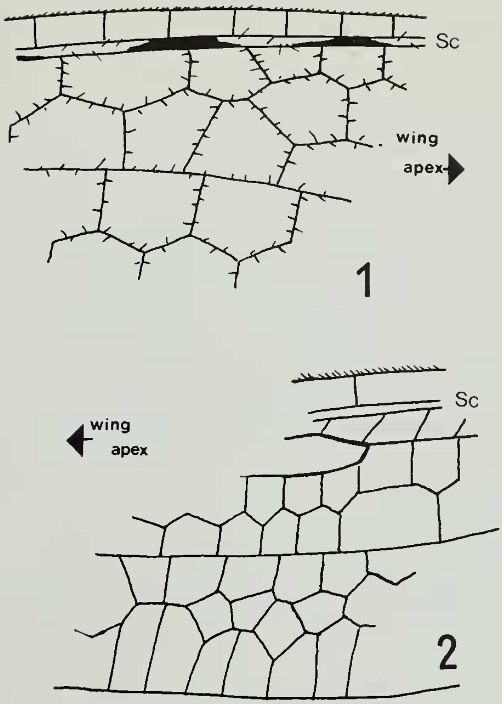
This family, including the fossils, was monographed by Meinander (1972); later he described other fossil species (Meinander 1975). One of the species he described is from Karatau (U.S.S.R.) and is generally regarded as Upper Jurassic; the other is from Siberian amber of Cretaceous age (Coniacian–Santonian). From this Siberian amber, younger than the Lebanese (Schlüter 1976), Meinander described a new genus and species of Coniopterygidae, *Glaesoconis cretica* (Aleuropteryginae), placing it in the tribe Fontenelleini. The new specimen from the Lebanese amber is congeneric with Meinander's species.

Glaesoconis fadiacra sp. nov.

Description. Front of head damaged. Flagellum with 19 segments, each slightly longer than broad. Maxillary palp five-segmented, apical segment large and broader than the others. Labial palps with enlarged terminal segment, number of labial segments unclear. Forewing about 1·7 mm (Fig. 3). Two crossveins in basal costal area. Sc_2 meeting R_1 basally of radial crossvein. Radial crossvein arises from fork of R_2+R_3. M_1 and M_2 fork, running separately to wing margin. Hindwing, partly obscured venation apparently similar to forewing. Apical r-m crossvein on branch M_1 of M_1+M_2. The abdomen is obscured but some evidence of the plicaturae on abdominal segments. [The genitalia are not visible in the specimen.]

Types. Holotype and Paratype: Lebanese amber, Lower Cretaceous. Coll. Professor Aftim Acra.

Discussion. There are three main characters which separate this species from *G. cretica*. The latter has more antennal segments (24–27). *G. fadiacra* has longer branches to R_2+R_3 and R_4+R_5,



Figs 1–2 Fragments of forewing, ? Myrmeleonid.

with their junction more basad, and the terminal segment of the maxillary palp is broader than the other segments.

With only two specimens available the validity of the intraspecific variation is uncertain. The presence of a separate M_1 on the wing margin, which is similar to *G. cretica*, is considered by Meinander to be a primitive character. In all Recent genera there are only two branches to the median vein, but three in *G. fadiacra* and *G. cretica*.

The difference between these fossil coniopterygids and Recent species is relatively small and all the main features of the family were evidently well established by the Lower Cretaceous. The presence of complex morphological features shows that the coniopterygid type of organization must have arisen well before the Lower Cretaceous, and the presence of a coniopterygid in

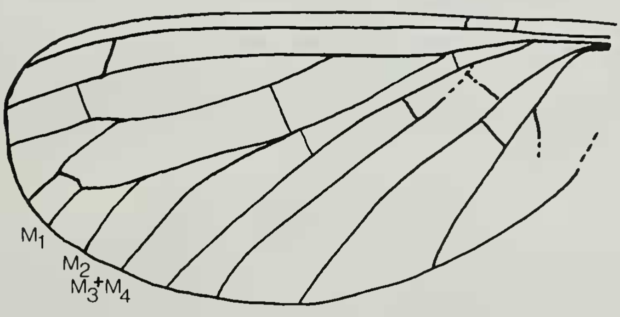


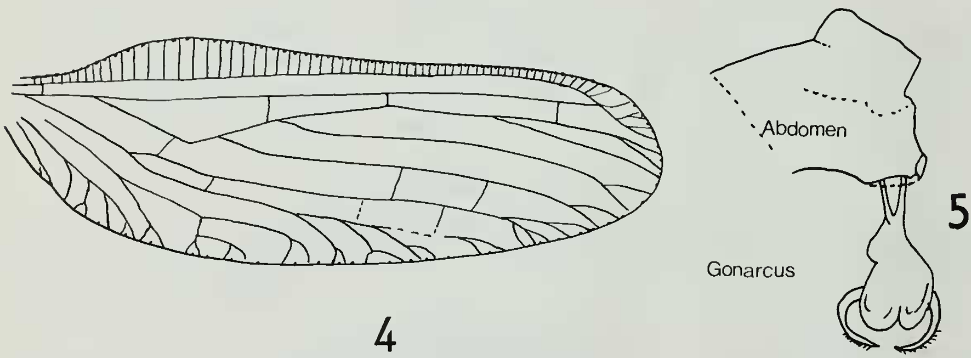
Fig. 3 Forewing, *Glaesoconis fadiacra* sp. nov. Coniopterygidae. See Fig. 7.

Upper Jurassic rocks (although with much less detail visible compared with the amber specimens) suggests an even earlier date for the separation of the Coniopterygidae from their sister group.

Family **BEROTHIDAE**

The characters given below suggest that both the adult specimens of the species described here are in the Osmyloidea (*sensu* Crowson *et al.* 1967). Riek (1970) divides the Osmyloidea, separating the Mantispoidea to include the Mantispidae, Sisyridae and Berothidae. One of the amber lacewings has characters which occur in both the Berothidae and the Sisyridae. Comparison of *Banoberotha enigmatica* sp. nov. with neuropterous fossils described from the Permian, Triassic and Jurassic does not provide any more information on its systematic position. Certainly *Permoberotha*, as illustrated by Carpenter (1954), is quite distinct.

The presence of unbranched costal veinlets in the fossil *B. enigmatica* is the most striking difference from Recent Berothidae. The hindwings are very similar, particularly with Cu_2 parallel to the hindwing margin. The anastomoses near the base of the hindwing in Recent Berothidae figured by Tjeder (1959) cannot be seen in the fossil. There are, however, sufficient characters for the fossil to be placed as a new genus and species in the Berothidae.



Figs 4–5 *Banoberotha enigmatica* gen. et sp. nov. Berothidae. Fig. 4, forewing. Fig. 5, apex of abdomen and gonarcus. See Fig. 8.

Genus ***BANOBEROTHA*** nov.

Type species. *Banoberotha enigmatica* sp. nov.

Generic diagnosis. Prothorax elongate. Forelegs cursorial. Forewing with costal veinlets unbranched. Rs and Sc fused near apex. Radial single with subparallel branches. MP bifurcate. Hindwing with Cu_2 parallel to hindwing margin.

Remarks. The separation of this genus from Recent berothid genera is based on the costal veinlets and the differences in cross venation (Fig. 4). While the branching or otherwise of the costal veinlets is variable within one species of Recent berothids, there are usually some veinlets that are forked. In *Banoberotha* all are unbranched. The genus is placed tentatively in the Nosybinae (MacLeod & Adams 1967).

Banoberotha enigmatica sp. nov.

Description. Male: Wing 6 mm, wingspan about 12·5 mm. Head damaged, eyes prominent. Mouthparts not clear. Antennae with circlet of hairs on each bead-like segment. Legs broken but very hairy. Prothorax at least twice as long as broad. Forewing (Fig. 4) with many macrotrichia on veins. No recurrent humeral vein. Trichosors all round wing margin. Costal margin broader near base. Radial and subcostal veins join near apex of wing. R_1 single with four roughly subparallel branches. MA from radial (*sensu* Martynov 1928), MP forked. Cubital branched. Anal veins not clear. Hindwing frenulum group of bristles. Cubital vein almost parallel to hindwing margin. Basal area indistinct. Abdomen damaged, posterior segments as in Fig. 5. This shows the gonarcus (?) forced out; its shape is distorted by fine air bubbles around it and the figure represents the best assessment of the outline of the structure.

HOLOTYPE. Male, Lebanese amber, Lower Cretaceous. Coll. Professor Aftim Acra.

DISCUSSION. This small fossil lacewing has been compared with examples of all the Recent families and with figures of all the fossil families currently regarded as neuropterous. The fossil shows clearly the specialization reached by the Lower Cretaceous Neuroptera. The frenulum, which can be clearly seen in the fossil, has not previously been seen in fossil specimens earlier than the Tertiary, because of problems of preservation. The whole insect, except for certain venation differences, has the appearance of a Recent berothid. The abdomen is not clear enough for detailed examination but its apical shape is indicated (Fig. 5), together with what may be the gonarcus. The latter has fine spines at the apex and may well have the arms as indicated in the figure, although the shape is distorted by the air present.

Banoberotha possesses characters of both berothids and sisyrids; the simple costal veinlets are typical of Sisyridae, but all the other characters, e.g. the branched median vein of the forewing and Cu_2 in the hindwing, are typical of the Berothidae. The elongate prothorax occurs in berothids but not in sisyrids, where the pronotum is broader than long. This elongate prothorax is similar to many hemerobiids, but the fossil lacks the recurrent humeral vein and the arrangement of the radial veins differs from that family.

Amongst the Lebanese amber material collected by Professor Acra is the larger part of a neuropterous larva (Figs 9–10). While some details of the abdomen are obscured, the mouthparts quite clearly suggest a berothid larva.

DESCRIPTION. Including the long mandibles, the larva is 6–8 mm long, very hairy, probably broader in the middle and with a relatively elongate prothorax. The mandibles are long and thin, while the maxillae are shorter but broader at the base, giving a distinctly triangular look to the mouthparts. Lateral ocelli are clear; each side has five ocelli, arranged in a half-circle of four plus one ocellus ventrally placed to this group. The antennae end in a fine seta, but the number of segments is not clear. The frons is rounded with four long hairs near the anterior margin. There is a prominent epicranial suture, and the labial palps are 4- or 5-segmented. The single apical tarsal segment preserved ends without a claw, but has a trumpet-shaped empodium.

DISCUSSION. The larvae of only a few Recent species of Berothidae are known, but the most important diagnostic feature is the broad bases to the maxillae (Riek 1970), which show clearly in the fossil. No evidence for the subfamily position of this larva can be deduced since adult lacewings from two distinct Berothid subfamilies have been found in the same amber.

The final specimen from the Lebanese amber, although damaged, shows most of the characters of the Berothidae, but especially the raptorial forelegs characteristic of the endemic African subfamily, Rhachiberothinae. It is distinct from the two Recent genera but still within the subfamily Rhachiberothinae, which evidently has a long fossil history.

Genus ***PARABEROTHA*** nov.

TYPE SPECIES. *Paraberotha acra* sp. nov.

GENERIC DIAGNOSIS. Prothorax not elongate, forelegs raptorial. Forewing with Sc and R joining near apex. Trichosors on wing margin. Subcostal veinlets branched in basal third.

REMARKS. From *Rhachiberotha* Tjeder the new genus is separated by the shorter pronotum and the fusion of Sc and R near the apex. It is similar to that genus in the more medial position of the antennal sockets. In the Recent genus *Mucroberotha* Tjeder these are placed higher up, level with the upper part of the eye. The genus *Paraberotha* is placed in the Rhachiberothinae; species in this subfamily are currently known only from Zimbabwe-Rhodesia.

Paraberotha acra sp. nov.

Description. Wing 4 mm. Head damaged, mouth parts missing, eyes prominent. Antennae with circlets of hairs on each segment, long, with bead-like, slightly elongate, segments. Pronotum broader than long. Tip of abdomen and most of legs missing. Forelegs raptorial (Fig. 12), with two rows of teeth on femur interlocking with spines on tibia and tarsi. Teeth 21–23 in each row on femur, 10–15 long spines on tibia. Probably 5 tarsal segments, 4 visible. First segment longer than rest with long spines, segments 2–3 enlarged apically with prominent spine. Wings partially obscured. Sc and R fused near apex, separate towards base. Costal veinlets bifurcate in basal third of forewing. No recurrent humeral vein. Hindwings partially obscured but Cu elongate, parallel to hind margin.

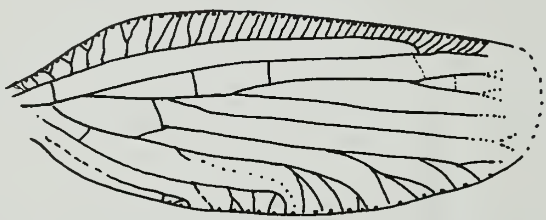


Fig. 6 Forewing, *Paraberotha acra* gen. et sp. nov. Berothidae. See Figs 11–12.

Holotype. Male (?), Lebanese amber, Lower Cretaceous. Coll. Professor Aftim Acra.

Discussion. Comparison of *Paraberotha acra* with the Recent species *Rhachiberotha signifera* Tjeder shows many interesting parallels and some differences. The forewing venation is broadly similar, but the Recent species has more subcostal veinlets bifurcating and Sc and R not fusing below the apex. The teeth of the femur are very similar in Recent and fossil species, especially in their construction and insertions, and differ only in the arrangement, being alternately long and short in the fossil while rather irregular in length, though in similar rows, in the Recent species. The arrangement of teeth on the femur differs amongst the few Recent species in the Rhachiberothinae.

The overall similarity of Recent and fossil species is striking. Probably one of the most fundamental differences is in the shape of the pronotum. In most Recent species (Mantidae, Mantispidae, Rhachiberothinae), where the forelegs are modified for grasping and holding the prey, the pronotum is elongate; in the fossil *Paraberotha* it is quite clearly not elongated.

Tjeder (1959) regarded the Rhachiberothinae as a possible connecting link between the Mantispidae and Berothidae. MacLeod & Adams (1967) review this relationship in more detail and, while not agreeing with the reasons given by Tjeder, agree with his conclusions and this possible relationship.

Apart from Lebanese amber, fossil Berothids are known only from Baltic amber (Eocene/Oligocene); these are probably in the Berothinae (MacLeod & Adams 1967). Schlüter (1978) describes *Retinoberotha stuermeri* as a new genus and species from the Cenomanian of north-west France.

Little is known of the biology of Recent Berothidae. For example, while the forelegs of Recent Rhachiberothinae are typically raptorial and are almost certainly used to catch prey, this has not actually been observed, and the modifications of the legs might even be used to assist in courtship, although I believe this unlikely.

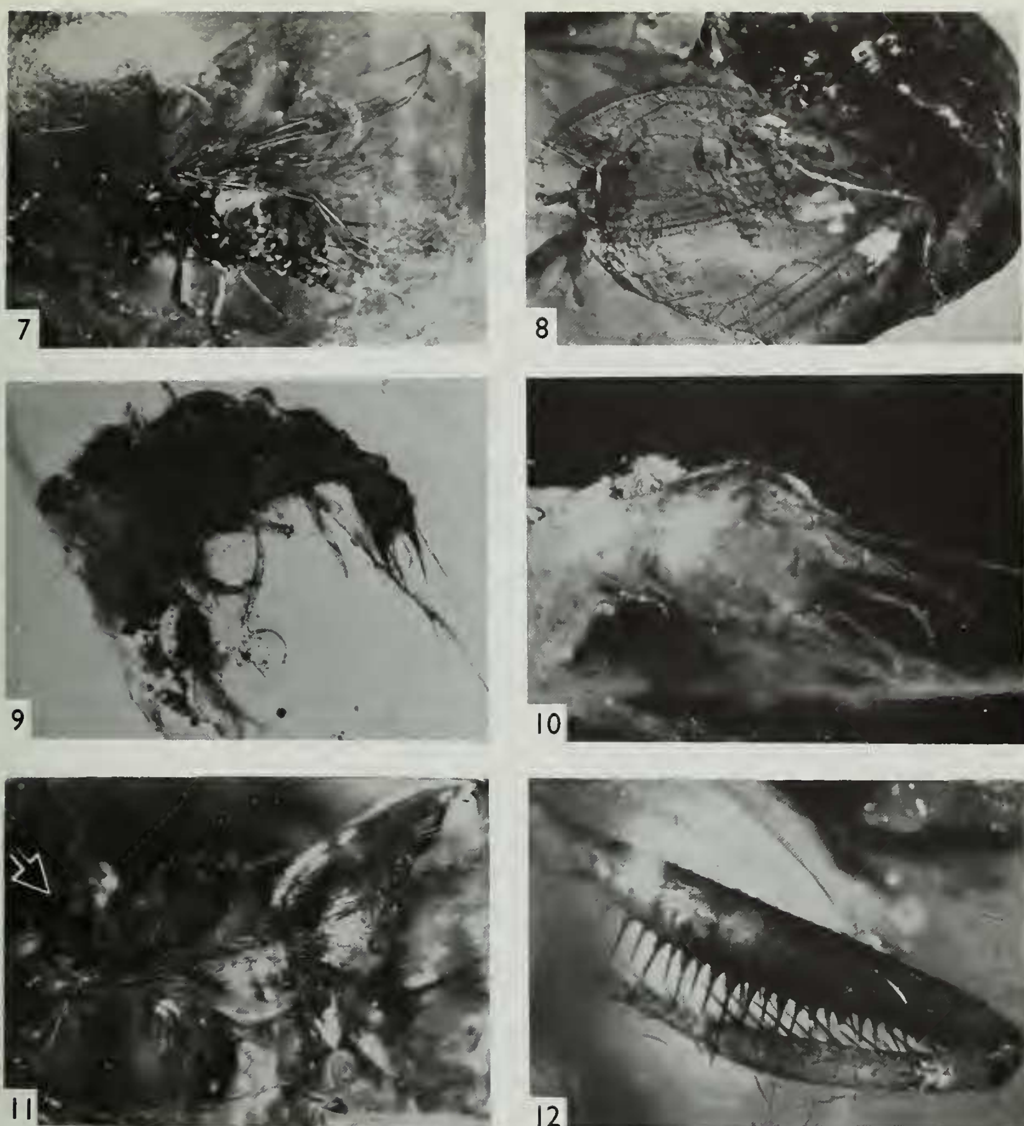


Fig. 7 *Glaesoconis fadiacra* sp. nov. See Fig. 3.

Fig. 8 *Banoberotha enigmatica* gen. et sp. nov. See Figs 4–5.

Figs 9–10 Berothid larva. Fig. 10, enlargement of mouth parts.

Figs 11–12 *Paraberotha acra* gen. et sp. nov. Fig. 11, head and raptorial foreleg (arrowed) on left. Fig. 12, enlargement of foreleg. See Fig. 6.

When considering the faunal and floral changes since the Lower Cretaceous, the morphological stability of the Nosybinae and Rhachiberothinae is apparent. It is possible that this very stability also accounts for their apparent rarity in Recent faunas and their extremely limited distribution; while the Berothinae are widespread throughout the world, although not abundant, the Recent Rhachiberothinae and Nosybinae are rare and restricted to central and southern Africa.

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